Soil movement by burrowing mammals: a review comparing excavation size and rate to body mass of excavators

Natalie S Haussmann

Department of Geography, Geoinformatics and Meteorology, University of Pretoria, South Africa

Corresponding author:

Natalie S Haussmann, Department of Geography, Geoinformatics and Meteorology, University of Pretoria, Private Bag X20, Hatfield, South Africa.

Email: natalie.haussmann@up.ac.za

Tel: +27 (21) 420 4049

Abstract

Mammal burrowing plays an important role in soil translocation and habitat creation in many environments. As a consequence, many burrowing mammals have at some point been studied in an ecosystem engineering context. From a geomorphological point of view, one of the focus areas of burrowing mammal research is on the amount of soil that is excavated and the rate at which this happens. As such, reviews exist on the volumes and rates of sediment removal by burrowing mammals in specific environments or for specific groups of species. Here a standardised comparison of mammal burrowing across a broad range of burrowing mammal species and environments is provided, focussing on both burrow volume and excavation rate. Through an ISI Web of Science-based literature search, articles presenting estimates of burrow volumes and/or excavation rate were identified. Relationships between species body size and burrow volume/excavation rate were explored and the influence of sociality and method of burrow volume estimation was assessed. The results show that, although bigger species construct

bigger burrows, it is the smaller species that remove more sediment per unit time at larger, site-level spatial scales. Burrow volume estimates are, however, independent of species sociality (solitary vs group-living) and method of burrow volume estimation (excavation-based vs mound-based). These results not only confirm previously established relationships between species body size and burrow volume, but, more importantly, they add to this, by exploring larger scale impacts of burrowing mammals along a body size gradient.

Keywords

Biogeomorphology, burrow, digging, denning, ecosystem engineer, mammal disturbance, sediment movement

I Introduction

Many mammal species excavate soil for shelter, nesting or foraging and consequently many studies exist on a range of impacts for a variety of burrowing mammals. The aims of such studies differ, depending on the discipline. From an ecological perspective, changes in plant and animal species richness, diversity and abundance are associated with burrowing and these changes differ in direction and magnitude (Root-Bernstein and Ebensperger, 2013). In central Spain, for example, increased burrowing by the European rabbit, *Oryctolagus cuniculus*, is positively correlated with increased lizard density and diversity (Bravo et al., 2009), whereas eradication of the same rabbit species leads to increased lizard numbers in the arid shrublands of Australia (Read et al., 2011). Such ecological changes, regardless of their direction, have led to many burrowing mammal species being placed within the ecosystem engineering/keystone species

context (e.g. Bragg et al., 2005; Whittington-Jones, 2006; Davidson et al., 2008; Bravo et al., 2009; Desbiez et al., 2013).

One of the focus areas of the geomorphological publications on mammal burrowing is on the amount of soil that is excavated and/or the rates at which this happens. As such, reviews exist on the volumes and rates of sediment removal by burrowing mammals in specific environments (see Kinlaw, 1999; Whitford and Kay, 1999 for reviews on arid environment burrowing) or by specific groups of species (see Smallwood and Morrison, 1999 for a review on pocket gopher). However, a comprehensive review, spanning different environments and different groups of burrowing species is still lacking. One of the main reasons for this is probably because reporting measures and methods are not standardised, making comparisons between studies difficult.

Studies on excavation volumes and/or rates often differ in terms of what they actually report. Some studies, for example, report the average size of an individual excavation, i.e. individual burrows, dens or foraging pits (e.g. Butler, 1992). This is useful when comparing which species create larger excavations. However, some animals might make large holes, but only create a few (e.g. aardvark in certain environments, see Whittington-Jones, 2006), whereas other animals make many small holes (e.g. house mice on Marion Island, Eriksson and Eldridge, 2014). In addition, some sites might seem very active, because there are many excavations, when their burrows are just older. Burrow longevity can differ significantly between habitat types, as a result of environmental conditions (Bragg et al., 2005). If one really wants to compare the geomorphological potential of burrowing animals at larger scale levels, spatial, and ideally also temporal standardisation is therefore necessary. Consequently, some studies report sediment removal per unit land area (Sawyer et al., 2012) or, ideally, sediment removed per unit land area per unit time (e.g. Bragg et al., 2005, Coombes and Viles, 2015).

In addition to reporting different measures, the units in which measurements are made also differ. Some older papers report in tons and acres (e.g. Ellison, 1946; Ingles, 1952), whereas the majority of the more recent publications report in SI units. The methods used to estimate the size of excavations are also inconsistent. Whereas some studies use the actual excavation to estimate burrow volumes (e.g. Sawyer et al., 2012; Eriksson and Eldridge, 2014), others estimate this from the size of the resulting debris mound (Borchard and Eldridge, 2011; Coombes and Viles, 2015). Lastly, some studies report on burrows, i.e. structures dug for nesting and denning (e.g. Sawyer et al., 2012; Coombes and Viles, 2015), whereas others report on foraging pits (e.g. Bragg et al., 2005), constructed for feeding and yet others report on underground structures used for both (Šklíba et al., 2010). Obviously, the definition of what exactly was measured and how this was defined needs to be standardised for comparisons to be meaningful.

From a biogeomorphological perspective, some of the interesting burrowing mammal-related questions are associated with species and environmental traits, and how these influence burrow characteristics. Using published measurements of burrow dimensions, Woolnough and Steele (2001) showed that larger burrow volumes were positively correlated with larger body mass. The potential role of variables other than body size in determining geomorphological measures of burrow impact, such as excavation size, has, however, been poorly explored (but see Root-Bernstein and Ebensperger, 2013 for such an analysis of ecological impacts of burrowing).

The aim of this paper is therefore to provide a standardised comparison of mammal burrowing across burrowing species and environments, focussing on both burrow volume (i.e. total volume of an individual underground cavity) and excavation rate (volume of soil removed per unit land per unit time). Through an extensive literature search, the 34 burrow volume estimates of Woolnough and Steele (2001) are supplemented with an update of excavation

volume studies from the past 15 years. In addition, factors other than body size (e.g. species sociality, method of burrow volume estimation) are explored as potential predictors of burrow volumes and excavation rates. Lastly, although the focus of this study was on structures made for nesting or denning, measurements of diggings for food were also recorded.

II Data and methods

1 Data set

An existing collection of papers on burrowing animals was used as a starting point for the literature search. From these articles, references within these articles, and discussions with a zoologist (McIntyre, 2015, personal communication), a list of burrowing mammal "group names" was compiled. These group names (e.g. pocket gopher), differed from both scientific names (e.g. *Geomys attwateri*) and common names (e.g. Attwater's pocket gopher). This list is believed to represent the major, well-known burrowers (i.e. mammals that burrow, regardless of the purpose of their burrowing). In addition, other, less-studied mammals were also included when encountered in the literature. Animals that do not dig their own burrows were only included if the species is well-known to substantially enlarge the burrow of the original digger (e.g. aardwolf are known to enlarge burrows of springhare). Based on this list, a search was conducted in ISI Web of Science using the term "burrow" combined with the group name of the mammals on the list. In this manner, "pocket gopher" would pick up on all species of pocket gopher and, similary, "mole-rat" would be picked up by both the search terms "mole" and "rat".

The abstracts of all papers from the resulting search outputs were subsequently scanned. Only those studies that reported either an estimate of burrow volume (or mass of the soil removed from the burrow) or of the soil displacement rate were included in the final database. If

volumes of soil displaced or movement rates did not appear in the abstract, but the title suggested that they could have been estimated, the methods and results sections of the papers were additionally studied. Furthermore, references in papers were examined and were also included in the database if burrow volume or sediment movement estimates were reported. Although the focus of this study was on structures made for nesting or denning (referred to as burrows), measurements of diggings for food (also known as foraging pits) were recorded separately where encountered in the literature.

Many studies recorded burrow dimensions (e.g. width, height, length, tunnel diameter) without explicitly estimating volumes or rates of sediment removal. Smallwood and Morrison (1999) used published burrow dimensions from pocket gopher studies to calculate burrow volumes, substituting missing dimensions with averages from other studies. Such calculations involve the assumption that burrows of all species share a similar shape. Whereas this may be the case for different species of pocket gopher, it certainly is not the case for all burrowing mammals. As the burrow shape that is assumed during calcucations can have a significant effect on the volume of soil calculated (Bancroft et al., 2004), and an in-depth study of different species' burrow shapes was not feasible, burrow volumes were not calculated from dimensions. Studies that did not explicitly mention either soil movement volumes or rates of displacement were therefore excluded from the database. However, when total volumes of sediment displaced were provided (e.g. in m^3 per ha) in combination with the density of burrows (count per ha), the average volume per burrow was calculated from these values. Similarly, where an estimate of the number of mounds constructed per year was provided, along with the size of an individual mound, excavation rates were calculated.

In addition to the studies selected from the literature search, the estimates by Woolnough and Steele (2001) were included in the final data base. This enabled a comparison of the burrow volume estimates from studies from the literature search with those of Woolnough and Steele (2001).

2 Variables recorded

From each of the papers the following variables were recorded: 1.) the study area, 2.) the excavation volume (m^3) and/or 3.) the excavation rate (m^3 ha^{-1} $year^{-1}$), and 4.) the method used to determine the excavation volume and/or rate. If more than one excavation volume and/or rate was provided, the mean was calculated. Estimates reported in units other than those used here (e.g. tons, acres) were converted. For studies estimating mass of soil removed from burrows, a typical topsoil bulk density value of 1.3 g per cm^3 (Lewis, 2008) was used (unless another density was specified) to convert these to volumes. Lastly, for each species, the average body mass of an adult female, as well as the social behaviour of the species (group-living vs. solitary), was also recorded. Although a range of mammalian social systems exists, a simplified, dichotomous distinction between solitary species (i.e. where adults live alone) and group-living species (where individuals live in discrete groups) was used. Some of the estimates from Woolnough and Steele (2001) were from unpublished sources, or general mammal text books, providing information on many species and studies. In such cases, only Woolnough and Steele's estimates were reported and used for analyses, and study areas and methods were reported as "unknown".

3 Statistical analyses

The effects of species body mass, sociality and method of burrow volume estimation on burrow volume were assessed by fitting a series of generalized linear models (GLMs) in the R statistical environment (R Version 3.1.2, R Core Team 2014). Both Gamma and Gaussian response models were considered, with identity-, log- and inverse-link functions. A stepwise procedure based on the Akaike's Information Criterion (AIC) was used to select amongst candidate models incorporating both untransformed and log-transformed predictors. Both the AIC and an examination of residuals from the fitted model showed that a Gaussian GLM with an identity-link function was the most appropriate model for burrow volume as a function of animal body size, sociality and the method used to determine burrow volume. Both burrow volume and body mass were log-transformed in the final model. Significance of best-fit model terms was tested using an F-test. The relationships between body mass and burrow rate, and body mass and digging volume were analysed using standard linear regression.

III Results

Rodents, and more specifically pocket gophers and mole-rats, are the most studied groups of mammal species when it comes to burrow volumes and excavation rates (Table 1). The 37 papers that were selected through the literature search, combined with the 34 estimates from Woolnough and Steele (2001) resulted in 74 entries that reported excavation volumes and/or rates for 53 mammal species (Table 1). Of the 74 entries, 61 were for burrows and 13 for diggings (Table 1). Of the 61 burrow entries, 47 estimated the volume of individual excavations (inlcuding Woolnough and Steele's estimates), six provided estimates of excavation rates and an additional eight provided both excavation volumes and rates. For the digging-related estimates, seven

Table 1. The 74 entries resulting from the literature search combined with the estimates from Woolnough and Steele (2001).

Species	Body mass (kg)	Sociality	Study area	Mean excavation volume (m^3)	Excavation rate ($m^3.ha^{-1}.year^{-1}$)	Method for determining excavation volume	Reference
Burrows							
Canis lupus Wolf	24[1]	Group-living[2]	Field laboratory	0.213		EDE	Ryon, 1977[b]
Canis latrans Coyote	14.6[1]	Group-living[2]	Unknown	0.908		Unknown	Ryon, 1986[b]
Otocyon megalotis Bat-eared fox	4.12[1]	Group-living[3]	Unknown	0.251		Unknown	Skinner and Smithers, 1990[b]
Hyaena brunnea Brown hyena	44.1[1]	Group-living[3]	Kalahari Desert	0.907		ED	Owens and Owens, 1979[b]
Crocuta crocuta Spotted hyena	73.6[1]	Group-living[3]	Unknown	2.36		Unknown	Kruuk, 1972[b]
Proteles cristatus Aardwolf	9.7[1]	Solitary[3]	Unknown	0.672		Unknown	Richardson, 1985[b]
Meles meles European badger	9.9[1]	Group-living[4]	Brighton, UK	15		EDE	Roper et al., 1991
Meles meles European badger	9.9[1]	Group-living[4]	Not mentioned	4.9		EDE	Roper, 1992
Meles meles European badger	9.9[1]	Group-living[4]	Oxford, UK	12	0.03	DD	Coombes and Viles, 2015
Ursus arctos horribilis Grizzly bear	100[1]	Solitary[2]	Glacier National Park, USA	4.3		ED	Butler, 1992
Condylura cristata Star-nosed mole	0.04[1]	Solitary[2]	Unknown	0.094		Unknown	Hickman, 1983[b]
Talpa europaea European mole	0.09[1]	Solitary[4]	Netherlands		3.37	DW	Wijnhoven et al., 2006
Oryctolagus cuniculus European rabbit	1.6[1]	Group-living[4]	Scotland	0.0495		EDE	Kolb, 1985
Vombatus ursinus Bare-nosed wombat	26[1]	Solitary[5]	Kangaroo Valley, Australia	1.4		DD	Borchard and Eldridge, 2011

Species	Body mass (kg)	Sociality	Study area	Mean excavation volume (m^3)	Excavation rate ($m^3.ha^{-1}.year^{-1}$)	Method for determining excavation volume	Reference
Vombatus ursinus Bare-nosed wombat	26[1]	Solitary[5]	Unknown	2.74		Unknown	Troughton, 1941[b]
Lasiorhinus krefftii Northern hairy-nosed wombat	26[1]	Solitary[5]	Unknown	5.73		Unknown	Steele and Temple-Smith, 1998[b]
Ornithorhynchus anatinus Platypus	1.44[1]	Solitary[5]	Unknown	0.078		Unknown	Burrell, 1927[b]
Heterocephalus glaber Naked mole-rat	0.02[6]	Group-living[6]	Laboratory	2.9		DV	Jarvis and Sale, 1971
Heterocephalus glaber Naked mole-rat	0.02[6]	Group-living[6]	Unknown	0.946		Unknown	Davies and Jarvis 1986, Bennett and Faulkes, 2000[b]
Bathyergus suillus Cape dune mole-rat	0.63[1]	Solitary[3]	Western Cape, South Africa	1.2600		DW	Thomas et al., 2009
Bathyergus suillus Cape dune mole-rat	0.63[1]	Solitary[3]	Unknown	2.01		Unknown	Davies and Jarvis, 1986[b]
Heliophobius argenteocinereus Silvery mole-rat	0.09[1]	Solitary[6]	Southern Malawi	0.0008[2]		EDE	Škliba et al., 2010
Heliophobius argenteocinereus Silvery mole-rat	0.09[1]	Solitary[6]	Athi Plains, Kenya	0.092		EDE	Jarvis and Sale, 1971[b]
Cryptomus hottentotus Common mole-rat	0.088[1]	Group-living[3]	Unknown	0.512		Unknown	Davies and Jarvis, 1986, Bennett, unpublished[b]
Georychus capensis Cape mole-rat	0.18[1]	Solitary[3]	Unknown	0.241		Unknown	Davies and Jarvis, 1986, Bennett, unpublished[b]
Tachyoryctes macrocephalus Big-headed mole-rat	0.597[1]	Solitary[6]	Abakkara, Ethiopia	0.275		EDE	Yalden, 1975[b]
Tachyoryctes splendens	0.218[1]	Solitary[6]	Mount Kenya	0.057		EDE	Jarvis and Sale, 1971[b]

Species	Body mass (kg)	Sociality	Study area	Mean excavation volume (m^3)	Excavation rate ($m^3.ha^{-1}.year^{-1}$)	Method for determining excavation volume	Reference
East African mole-rat *Tachyoryctes splendens ruandae*	0.212[1]	Solitary[6]	Unknown	0.1005		Unknown	Rham, 1980[b]
Ruanda mole-rat *Ctenomys opimus*	0.28[1]	Group-living[7]	Unknown	0.297		Unknown	Davies and Jarvis, 1986[b]
Highland tuco-tuco *Thomomys bottae* and *Thomomys umbrinus*	0.16[1,a]	Solitary[2]	Chihuahuan and Sonoran desert	0.006		DD	Kerley et al., 2004
Pocket gopher *Thomomys bottae*	0.12[1]	Solitary[2]	California, USA	0.0043	40	DV	Gabet, 2000
Botta's pocket gopher *Thomomys bottae*	0.12[1]	Solitary[2]	California, USA		21.95	DW	Cox, 1990
Botta's pocket gopher *Thomomys bottae*	0.12[1]	Solitary[2]	California, USA	0.0011	3	DV	Black and Montgomery, 1991
Botta's pocket gopher *Thomomys bottae*	0.12[1]	Solitary[2]	Laboratory	0.029		DW	Vleck, 1979[b]
Botta's pocket gopher *Thomomys monticola*	0.07[8]	Solitary[2]	California, USA		14.42	DW	Ingles, 1952
Mountain pocket gopher *Thomomys talpoides*	0.13[1]	Solitary[2]	Utah, USA		9.6	DW	Ellison, 1946
Northern pocket gopher *Geomys attwateri*	0.136[1]	Solitary[2]	Texas, USA	0.058		EDE	Cameron et al., 1988[b]
Attwater's pocket gopher *Geomys breviceps brazensis*	0.4[2]	Solitary[2]	Texas, USA		7.15	DD	Buechner, 1942
Pocket gopher							

Species	Body mass (kg)	Sociality	Study area	Mean excavation volume (m^3)	Excavation rate ($m^3.ha^{-1}.year^{-1}$)	Method for determining excavation volume	Reference
Geomys bursarius Plain's pocket gopher	0.164[2]	Solitary[2]	Unknown	0.155		Unknown	Thorne and Andersen, 1990[b]
Geomys pinetis Southeastern pocket gopher	0.14[1]	Solitary[2]	Florida	0.319		Unknown	Davies and Jarvis, 1986[b]
Pappogeomys castanops Yellow-faced pocket gopher	0.326[1]	Solitary[2]	Texas, USA	0.619		EDE	Hickman, 1977[b]
Dipodomys spectabilis Banner tailed kangaroo rat	0.18[1]	Solitary[2]	Chihuahuan desert	0.0138		DD	Andersen and Kay, 1999
Mus Musculus House mouse	0.02[1]	Group-living[4]	Marion Island, sub-Antarctic	0.0003	20.6	ED	Eriksson and Eldridge, 2014
Mus Musculus House mouse	0.02[1]	Group-living[4]	Marion Island, sub-Antarctic	0.0017		EDE	Avenant and Smith, 2003
Mus Musculus House mouse	0.02[1]	Group-living[4]	Laboratory	0.0003		EDE	Bouchard and Lynch, 1989
Mus Musculus House mouse	0.02[1]	Group-living[4]	Laboratory	0.0022		EDE	Schmid-Holmes et al., 2001
Rattus villosissimus Long-haired rat	0.14[1]	Group-living[5]	South-western Queensland	0.353		EDE	Predavec and Dickman, 1994[b]
Desmodillus auricularis Namaqua gerbil	0.05[1]	Group-living[3]	Kalahari desert	0.012		EDE	Nel, 1967[b]
Microtus ochrogaster Prairie vole	0.04[1]	Group-living[2]	Kentucky, USA	0.017		EDE	Davis and Kalisz, 1992[b]
Otomys sloggetti robertsi African ice rat	0.14[1]	Group-living[9]	Sani-valley, Lesotho	0.0057		EDE	Hinze et al., 2006
Saccostomus campestris Pouched mouse	0.047[1]	Solitary[3]	South Africa	0.0036		EDE	Ellison, 1993[b]
Gerbillurus paeba Hairy-footed gerbil	0.025[1]	Group-living[3]	Unknown	0.032		Unknown	de Graaff and Nel, 1965[b]

Species	Body mass (kg)	Sociality	Study area	Mean excavation volume (m^3)	Excavation rate ($m^3.ha^{-1}.year^{-1}$)	Method for determining excavation volume	Reference
Pedetes capensis Springhare	3.23[1]	Solitary[3]	Botswana	1.282		EDE	Butynski and Mattingly, 1979[b]
Spermophilus saturatus Arctic ground squirrel	0.22[2]	Group-living[2]	Yukon, Canada	0.07	15.4	DD	Price, 1971
Spermophilus columbianus c. Columbian ground squirrel	0.58[1]	Group-living[2]	Canadian Rockies, Canada	0.02	1.05	DW	Smith and Gardner, 1985
Tamias striatus Eastern chipmunk	0.086[1]	Solitary[2]	Louisiana, USA	0.011		EDE	Thomas, 1974[b]
Rodents (voles, marmot, ground squirrel)	Too variable	Group-living[2]	Canadian Rockies, Canada	0.0053	2	DD	Hall et al., 1999
Rodents (voles, marmot, ground squirrel)	Too variable	Group-living[2]	Canadian Rockies, Canada		0.0994	DD	Hall and Lamont, 2003
Various (voles and moles)	Too variable	Too variable	Luxembourg Ardenne, Luxembourg	0.001	19.4	DD	Imeson, 1976
Orycteropus afer Aardvark	46.3[1]	Solitary[3]	Unknown	1.74		Unknown	Taylor and Skinner, 2003[b]
Dasypus novemcinctus Nine-banded armadillo	3.8[1]	Solitary[2]	Alabama, USA	0.0345		ED	Sawyer et al., 2012
Diggings							
Ursus arctos horribilis Grizzly bear	100[1]	N/A	Canadian Rockies, Canada		4.66	ED	Hall and Lamont, 2003
Ursus arctos horribilis Grizzly bear	100[1]	N/A	Yellowstone National Park, USA	0.05		ED	Mattson, 2004
Ursus arctos horribilis Grizzly bear	100[1]	N/A	Glacier National Park, USA	0.5		ED	Butler, 1992

Species	Body mass (kg)	Sociality	Study area	Mean excavation volume (m^3)	Excavation rate ($m^3.ha^{-1}.year^{-1}$)	Method for determining excavation volume	Reference
Taxidea taxus American badger	8.6[1]	N/A	Idaho, USA	0.026	3.9	DD	Eldridge, 2004
Hystrix indica Indian crested porcupine	15.4[1]	N/A	Negev desert, Israel	0.0003	0.26	ED	Shachak et al., 1991
Hystrix africaeaustralis Cape Porcupine	13.7[1]	N/A	Western Cape, South Africa	0.0005	1.6	ED	Bragg et al., 2005
Bettongia lesueur and *Macrotis lagotis* Burrowing bettong and greater bilby	1.6[1,a]	N/A	Eastern Australia	0.0099		ED	Eldridge et al., 2012
Bettongia lesueur and *Macrotis lagotis* Burrowing bettong and greater bilby	1.6[1,a]	N/A	South Australia	0.0022		ED	James and Eldridge, 2007
Bettongia penicillata Brush-tailed bettong	1.3[1]	N/A	Western Australia	0.0002	1.6	DD	Garkaklis et al., 2004
Tachyglossus aculeatus Short-beaked echidna	3.5[1]	N/A	Eastern Australia	0.0096		ED	Eldridge et al., 2012
Oryctolagus cuniculus European rabbit	1.6[1]	N/A	South Australia	0.0012		ED	James and Eldridge, 2007
Oryctolagus cuniculus European rabbit	1.6[1]	N/A	South Australia	0.0013	3.28	DD	James et al., 2011
Heteromyid rodents	Too variable	N/A	Chihuahuan desert	0.0002		ED	Eldridge et al., 2012

Body mass values are averages for adult females. Data are from [1]Silva and Downing, 1995; [2]Feldhamer et al., 2003; [3]Skinner and Smithers, 1990; [4]van den Brink, 1967; [5]Jackson, 2003; [6]Jarvis and Sale, 1971; [7]Anacker and Beery, 2013; [8]Ingles, 1952; [9]Hinze, 2005.
[a]Average of species taken; [b]from Woolnough and Steele, 2001.
ED: measured burrow/digging dimensions without excavation; EDE: measured burrow/digging dimensions through excavation; DD: measured dimensions of debris resulting from excavation; DW: weighed debris resulting from excavation; DV: volume of debris determined with a measuring jug.

studies reported digging volumes, one reported the excavation rate as a result of digging and five reported both volumes and rates.

Five studies were performed in laboratories or field set-ups outside of the animal's natural habitat, and one further study did not report the study site. An additional 17 study areas were entered as "unknown". Studies from South America and Asia seem to be largely lacking. The methods that were generally employed to estimate excavation volumes were based on either measuring the excavation itself or the debris resulting from the excavation (Table 1). However, burrow volume was independent of the method of estimation (GLM, $F_{1,31} = 0.27$, $p = 0.61$).

The results support the trend found by Woolnough and Steele (2001) that bigger species have bigger burrows (Figure 1, GLM, $F_{1,33} = 35.2$, $p < 0.001$). As expected, the trend for diggings follows that of burrows, i.e. bigger species also construct bigger diggings (Figure 1, $r^2 = 0.47$, $F_{1,9} = 9.85$, $p = 0.01$). The largest burrows in volume are constructed by social groups of European badgers, followed by the northern hairy-nosed wombat and the grizzly bear (Figure 1). Of the smaller mammal species, the naked mole rat constructs the largest burrows. For a given body size, group-living species and solitary species' burrows do not differ significantly in size (GLM, $F_{1,33} = 0.25$ $p = 0.62$). Lastly, in contrast to the findings for burrow volumes, excavation rates showed the opposite trend. For a given land area, bigger species remove less sediment per year than smaller species (Figure 2, $r^2 = 0.73$, $F_{1,9} = 23.9$, $p < 0.001$).

IV Discussion

The relationship between species' body size and burrow volume, based on indvidual authors' estimates of burrow volume, is consistent with those of Woolnough and Steele (2001). Therefore, as expected, bigger species dig bigger burrows (see also Vleck, 1981; Van Vuren and

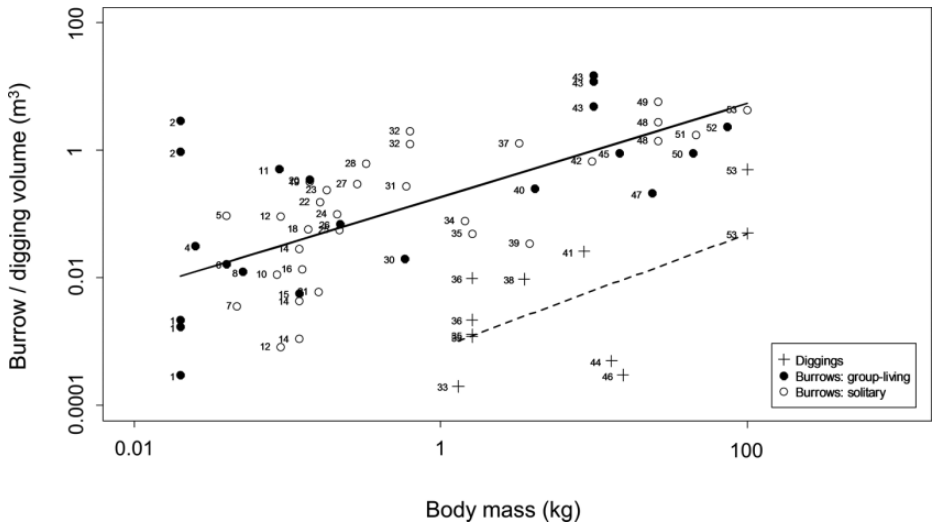

Figure 1. Relationship between body mass and burrow volume, distinguishing between solitary and group-living species' burrows, as well as diggings. Results show that there is a significant positive relationship between body mass and both burrow volume (generalised linear model, $F_{1,33} = 35.2$, $p < 0.001$, solid line) and digging volume ($r^2 = 0.47$, $F_{1,9} = 9.85$, $p = 0.01$, dotted line). Species are as follows: 1. *Mus Musculus*, 2. *Heterocephalus glaber*, 4. *Gerbillurus paeba*, 5. *Condylura cristata*, 6. *Microtus ochrogaster*, 7. *Saccostomus campestris*, 8. *Desmodillus auricularis*, 10. *Tamias striatus*, 11. *Cryptomys hottentotus*, 12. *Heliophobius argenteocinereus*, 14. *Thomomys bottae*, 15. *Otomys sloggetti robertsi*, 16. *Dipodomys spectabilis*, 18. *Geomys attwateri*, 19. *Geomys pinetis*, 20. *Rattus villosissimus*, 21. *Thomomys bottae* and *Thomomys umbrinus*, 22. *Geomys bursarius*, 23. *Georychus capensis*, 24. *Tachyoryctes splendens ruandae*, 25. *Tachyoryctes splendens*, 26. *Spermophilus saturatus*, 27. *Ctenomys opimus*, 28. *Pappogeomys castanops*, 30. *Spermophilus columbianus c*, 31. *Tachyoryctes macrocephalus*, 32. *Bathyergus suillus*, 33. *Bettongia penicillata*, 34. *Ornithorhynchus anatinus*, 35. *Oryctolagus cuniculus*, 36. *Bettongia lesueur* and *Macrotis lagotis*, 37. *Pedetes capensis*, 38. *Tachyglossus aculeatus*, 39. *Dasypus novemcinctus*, 40. *Otocyon megalotis*, 41. *Taxidea taxus*, 42. *Proteles cristatus*, 43. *Meles meles*, 44. *Hystrix africaeaustralis*, 45. *Canis latrans*, 46. *Hystrix indica*, 47. *Canis lupus*, 48. *Vombatus ursinus*, 49. *Lasiorhinus krefftii*, 50. *Hyaena brunnea*, 51. *Orycteropus afer*, 52. *Crocuta crocuta*, 53. *Ursus arctos horribilis.*

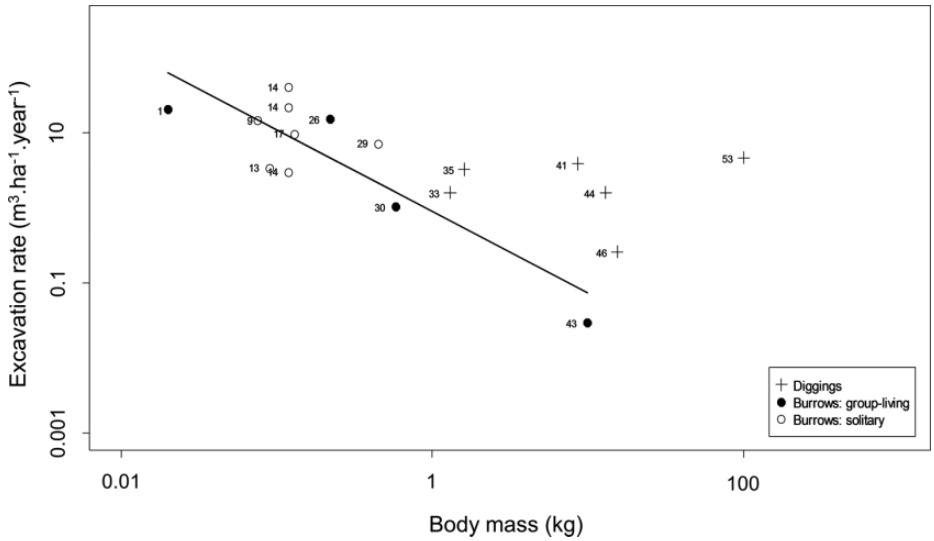

Figure 2. Relationship between body mass (*M*) and excavation rate (*E*), distinguishing between solitary and group-living species' burrows, as well as diggings. The equation for the relationship for burrows is $E = 0.9M^{-1.1}$ ($r^2 = 0.73$; SE = 1.11; $F_{1,9} = 23.9$; $n = 11$, $p < 0.001$). Species are as follows: 1. *Mus musculus*, 3. *Microtus arvalis*, 9. *Thomomys monticola*, 13. *Talpa europaea*, 14. *Thomomys bottae*, 17. *Thomomys talpoides*, 26. *Spermophilus saturatus*, 29. *Geomys breviceps brazensis*, 30. *Spermophilus columbianus c.*, 33. *Bettongia penicillata*, 35. *Oryctolagus cuniculus*, 41. *Taxidea taxus*, 44. *Hystrix africaeaustralis*, 46. *Hystrix indica*, 53. *Ursus arctos horribilis.*

Ordeňana, 2012). For a burrow to provide a practical nesting site or shelter, it obviously has to be larger than its occupant. However, the high initial energetic cost associated with burrowing (Vleck, 1979; Lovegrove, 1989) also means that most species do not construct burrows much larger than this minimum requirement (Woolnough and Steele, 2001).

Van Vuren and Ordeňana (2012) found that more highly social species of ground squirrel excavate longer burrow systems, supposedly to accommodate the additional occupants. In contrast, results from this study provide no support for a relationship between sociality and burrow size. A very likely explanation is that Van Vuren and Ordeňana (2012) used a five-point scale of sociality to categorise ground squirrel, wheras this study used the relatively crude distinction between solitary/group-living followed by Root-Bernstein and Ebensperger (2013). Although basic, such a dichotomous distinction of sociality can provide baseline information for comparitive studies (Lacey and Wieczorek, 2003). There are, however, many species that are considered group-living, but that do not share their burrow systems (e.g. wolf, coyote, hyena species) and are presumably therefore also solely responsible for their creation. Multiple diggers obviously have the potential to create larger excavations, especially where energetic costs are high (Jarvis et al., 1994; Lacey and Sherman, 1997; Bennett and Faulkes, 2000), but a rough division between solitary and group-living species presumably does not pick up on such patterns, whereas a more subtle subdivision representing a continuum of sociality categories, would. Indeed, in this study, the species that created burrow volumes disproportionate to their body size (e.g. naked mole rat, European badger) were highly social species and also share burrows between individuals (Jarvis and Sale, 1971; Kruuk, 1989; Coombes and Viles, 2015).

Smallwood and Morrison (1999) reviewed estimates of pocket gopher burrow volumes and excavation rates, and assessed the variation in such estimates between different methods

employed. They used both original estimates, as well as derived estimates, made by substituting average burrow dimensions for missing values. They found that original estimates did not differ significantly between methods, but that mound counts produced the largest derived estimates of both burrow volume and excavation rate. Results from this study support their findings of original estimates, i.e. whether the measurements were mound- or excavation-based did not affect burrow volume estimates. The vast majority of the studies that reported burrow excavation rates, however, used mound-based measurements. Similarly, most digging studies, used excavation-based measurements. A comparison between the two methods of estimation was therefore not possible for either burrow excavation rates or digging volumes.

An interesting, but relatively unexplored aspect of burrowing disturbance is the impact that burrowing mammals have at larger spatial and temporal scales and how that relates to body size. Results from this study add to those of Woolnough and Steele (2001) by shedding light on this relationship. According to the results presented here, the body size relationship found for burrow volume is inverted at site levels and thus, smaller species remove more soil per unit time and unit land area than their larger counterparts (Table 1). Smaller species therefore create more burrows than larger species, which offsets the effect of their reduced burrow size when it comes to site level sediment movement. Two potential explanations are offered for this increased number of burrows in the smaller species: 1.) smaller species occur in greater numbers and 2.) smaller species dig more excavations per individual per year.

An inverse relationship between species body size and local abundance has indeed been demonstrated (Damuth, 1981) and certainly helps to explain the site level results presented here. A hundred pocket gophers therefore have a bigger impact at a larger spatial scale than a single grizzly. However, the contribution of digging differences between individuals of varying body

size is not known, as data on sediment movement rates per individual animal are scarce. In general, burrowing has a larger energetic cost for large animals than for small animals (Vleck, 1981; Johnson, 1998) and intuitively one would therefore expect larger animals to construct fewer excavations per year than smaller animals. Again, as is the case for burrow size, sociality seems to have no effect on sediment movement rates (but note that the sample size is small and no formal statistical tests were possible). Therefore, although European badgers are group-living animals and create the largest individual excavations, their very low densities (Coombes and Viles, 2015) mean that they have a low impact at a larger site level. On the other hand, the solitary pocket gopher often occurs at high densities (Miller, 1964; Bandoli, 1987) and has a relatively large site level impact, despite creating small individual excavations. These results are perhaps in some ways analogous to Wolman and Miller's classic 1960 paper in which the cumulative effect of a geomorphic event is described as the product of the magnitude of the event and the frequency at which it occurs (Wolman and Miller, 1960). However, Wolman and Miller suggest that moderately sized events provide the most effective combination of magnitude and frequency, whereas the results presented here suggest that smaller mammal burrowers are the most effective geomorphic agents at site level spatial scales.

V Conclusion

In addition to standardising and integrating disparate publications on mammal burrowing, this paper highlights two important relationships: 1.) a positive relationship between species body size and burrow volume and 2.) a negative relationship between species body size and excavation rate. Although the relationship between species body size and burrow volume at the scale of individual excavations is interesting, it is at larger spatial scales, where excavation rates

are measured, that processes such as denudation and erosion are important. Whether or not the burrowing process in itself can be called erosion is perhaps debatable as the majority of mammal burrowers do not move the soil they excavate very far. However, burrowing contributes towards loosening and exposing soil, making it vulnerable to erosion. As such, the results presented here highlight the significance of smaller mammal burrowers in this loosening process, emphasizing their importance as geomorphic agents.

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